EXECUTIVE SUMMARY

RIPARIAN BIOLOGICAL DIVERSITY IN THE LAKE TAHOE BASIN

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This document presents the results of a four-year study of biological diversity in lotic and lentic riparian ecosystems in the Lake Tahoe basin. We examined the patterns of diversity of a range of taxonomic groups: birds, mammals, amphibians, invertebrates, vascular plants, and macrofungi. In addition, we analyzed habitat associations of certain species of particular interest to wildlife managers in the basin. Here, the results of the study and recommendations for the management of biological diversity in the basin are summarized. Citations have been removed; they are provided in the main document.

INTRODUCTION AND OBJECTIVES

Biological diversity can be defined as "the variety and variability among living organisms and the ecological complexes in which they occur." Current biological diversity is a result of a variety of environmental events and processes, including past evolutionary developments, biogeographic processes, extinctions, and current influences. This study focuses on patterns of composition and structure of species assemblages to better understand the past and present factors affecting biological diversity at the basin scale. The concept of biological diversity can be applied to a wide range of spatial and organizational scales, including genetic, species, community, and landscape. Diversity can be partitioned into 3 facets: alpha, beta and gamma diversity. Alpha diversity is the number of distinct taxa (e.g., species, genera, families) in a given location as defined by the researcher. Beta diversity is the degree to which species composition changes along an environmental gradient. Gamma diversity is variously interpreted as either (1) the rate at which additional species are encountered as geographical replacements within a similar environmental condition (e.g., vegetation zones) in different localities, or (2) regional diversity as determined by the sum total of species across many sample units. In the study of lotic riparian ecosystems, both alpha and beta diversity are addressed, and gamma diversity is treated as regional diversity, as defined by the total number of taxa occurring across all sample sites. In the study of lentic riparian ecosystems, only alpha diversity is addressed.

This study also addresses patterns of rarity. Rare taxa are those having low abundance or small ranges. Ecological communities tend to consist of a few relatively common species and many rare ones. Because each species is believed to occupy a unique niche, rare species then constitute not only the bulk of diversity in terms of species richness, but also represent a substantial proportion of the diversity of life history characteristics and functional roles in ecosystems. Although rarity is generally a poor predictor of extirpation or extinction, it is associated with a higher probability of extirpation and is commonly used as an indication of vulnerability to extirpation or extinction. Thus, the rare species in a given assemblage constitute a substantial contribution to the biological diversity of an area, and data on their composition and environmental correlates can provide insights into the factors influencing and vulnerabilities facing biological diversity. By definition, rare species are infrequently encountered and therefore they can be readily underrepresented or their associations masked by more common species in assessments of overall patterns of species richness. In the study of lotic riparian ecosystems, species rarely encountered in the study area are identified and analyzed in terms of their patterns of richness to elucidate their contributions to biological diversity.

Riparian ecosystems are some of the most productive and ecologically diverse ecosystems in California and the Sierra Nevada. For example, of the 401 species of mammals, birds, reptiles and amphibians in the Sierra Nevada, approximately 21% depend on riparian environments. Riparian environments are one of the least researched ecosystems relative to their contribution to biological diversity. Despite their importance, they are rarely mapped and, therefore, are commonly overlooked in land use planning exercises.

This effort was directed at 3 primary goals: 1) to describe patterns of biological diversity in lotic and lentic riparian ecosystems within a topographic basin; 2) to elucidate the environmental features and underlying processes potentially responsible for observed patterns; and 3) to provide information and interpretations useful in the conservation of biological diversity within the Lake Tahoe basin, as well as in other similar environments. In this study, we addressed a total of 6 major taxonomic groups—5 in lotic riparian ecosystems (birds, mammals, invertebrates, vascular plants, and macrofungi) and 3 in lentic riparian ecosystems (birds, amphibians, and littoral zone plants). Three primary questions were addressed in this study.

1. What are the primary environmental conditions and gradients within the study area?
2. What are the relationships of various facets of biological diversity (alpha diversity, rarity, and beta diversity in lotic riparian ecosystems; alpha diversity alone in lentic riparian ecosystems) with environmental conditions, gradients, and associated processes?
3. What implications do these relationships have for land management and the conservation of riparian biological diversity?

Chapters 1 through 10 of this document, including all the lotic riparian work, are the dissertation work of Patricia Manley. The remaining 2 chapters, including all the lentic riparian work, represent work jointly conducted by Patricia Manley and Matthew Schlesinger.

STUDY AREA AND METHODS

The study area was located in the Lake Tahoe basin, which occupies upper elevations and is dominated by upper montane and subalpine zones and mountain streams. The location of Lake Tahoe basin at a confluence of biogeographic zones results in a diversity of environmental conditions and a unique array of flora and fauna around the basin, as well as some distinct distributions of biota around the basin. A total of 312 vertebrates are residents or occur on a regular basis in the Lake Tahoe basin, including 217 birds, 59 mammals, 5 amphibians, 8 reptiles, and 23 fish. Over 5000 species of invertebrates are suspected to occupy the Lake Tahoe basin, including terrestrial and aquatic insects, mollusks, spiders, and crustaceans. A total of approximately 1300 vascular plant species potentially occur in the Lake Tahoe basin, with 1077 species having been confirmed. A list of potentially occurring macrofungi taxa compiled recently consisted of 339 genera, 60 of which have been documented as occurring in the basin.

A total of 80 stream reaches in 20 watersheds were used to describe lotic riparian conditions. Sample reaches were located randomly within randomly-selected watersheds. Lotic riparian sampling was conducted in 1995 and 1996. Lentic riparian conditions were assessed at 88 lentic units: lakes, small ponds, and wet meadows. Lentic units also were selected in a stratified random manner. Lentic riparian sampling was conducted in 1997 and 1998.

A variety of survey techniques were used. We surveyed birds using point counts. Mammals were surveyed using live-trapping, pitfall traps, and walking surveys. We surveyed amphibians and reptiles using visual encounter surveys. Invertebrates were surveyed with pitfall traps and sweepnet surveys. Walking surveys were employed to survey vascular plants and fungi. Environmental features were measured using a variety of field techniques and Geographic Information Systems analysis.

A variety of techniques were employed to analyze the data collected. Alpha diversity was represented by species richness. Patterns of richness with environmental variables were analyzed with correlation, stepwise multiple linear regression, and analysis of variance. Environmental gradients were identified through principal components analysis. Beta diversity (or species turnover) was based on shifts in species composition along environmental gradients as represented by species counts and Whittaker's index.

ENVIRONMENTAL CHARACTERISTICS OF LOTIC RIPARIAN ECOSYSTEMS

Key Findings

1. Two physical gradients were represented by the sample reaches: from low to high elevation and precipitation, and from narrow, straight, fast channel flow to wide, sinuous, slower channel flow. For a relatively small area, the basin has 'steep' gradients in abiotic environmental factors, represented in this study by elevation and precipitation.

2. Four vegetation gradients and one woody debris gradient were represented by the sample reaches. A gradient in lower elevation forest types (below the subalpine zone) from mixed conifer to lodgepole pine with meadow was the strongest gradient, followed by a gradient that followed elevation, from mixed conifer and lodgepole pine to subalpine conifer and shrubs. The third and fourth gradients were increasing amounts of alder–willow and aspen–cottonwood, respectively. The woody debris gradient represented increasing log and snag densities.

3. The lower elevation forest to meadow gradient was closely related to the channel flow gradient. The subalpine vegetation and snag and log gradients were closely related to the elevation–precipitation gradient, whereas the aspen–cottonwood gradient had an opposing relationship with the elevation-precipitation gradient.

4. Precipitation, channel gradient, sinuosity, width, all the forest and riparian vegetation types, large logs, small snags, and canopy cover all varied significantly by basin orientation. Precipitation, channel width, channel sinuosity, subalpine conifer, lodgepole pine, and large logs were all greater on the south and west sides compared to the north and east sides of the basin. In contrast, channel gradient and canopy cover index were greater on the north and east sides compared to the south and west sides of the basin. Mixed conifer, small snags, aspen–cottonwood, and alder–willow had similar patterns of association by orientation, being highest on the east and west, and lowest on the north and south.

Management Recommendations

1. Management for the conservation of biological diversity needs to consider the primary physical and biological gradients present in the basin. Together, elevation and precipitation are known to represent a complex interaction of environmental factors such as decreasing mean temperatures, decreasing growing season length, increasing precipitation, increasing wind speeds, and different soil properties at higher elevations. The channel flow gradient is interpreted as directly representing shifts in geomorphology (including increased

channel–floodplain interactions), and indirectly representing shifts in productivity and biological characteristics. The forest to meadow gradient is likely to represent a substantial proportion of the biological diversity in the basin. Further, the interspersion of conifer, shrub, and riparian vegetation on the sample reaches increases the species diversity and structural heterogeneity of the riparian environment, although it may have lower productivity than riparian environments comprised entirely of riparian vegetation. The interplay of productivity and heterogeneity are likely to result in complex relationships between biological diversity and vegetative conditions.

2. Most aspen stands in the Sierra Nevada are considered to be stable communities adapted to ecotonal areas between forest and meadows. A known exception to this is in some red fir forests, where aspen can appear as an early seral species. Fire is the most common form of disturbance that retains the presence of "seral" aspen stands. Fire suppression and grazing may have altered the extent and character of aspen stands in the basin. Investigating the effects of grazing and fire on aspen in the basin would provide valuable information on how to manage these activities to benefit aspen stands.

3. Fire typically prevents lodgepole pine from invading meadows as they dry out through succession, since mature lodgepole pine trees are often killed by fire. In the basin where fire has been suppressed for many decades, it is likely that lodgepole pine has become more prevalent throughout the basin, particularly in association with riparian and meadow environments. Reintroduction of fire as an ecosystem process in meadow as well as forest environments is likely to help maintain and restore a more representative distribution and abundance of lodgepole pine forests and meadows in the basin.

4. The Lake Tahoe basin is located in a transition zone between the climate and vegetation of the west slope of the Sierra and the Great Basin to the east. Precipitation and elevation are generally greater on the west side, and average temperatures are generally higher on the east side. Such strong gradients of variation among orientations are likely to influence the distribution of biota, potentially having a more pronounced influence on less mobile species because of the barriers that the environmental conditions of some orientations present. Management of any environmental feature, such as forest structure, fuels management, and stream or lake restoration, should take into consideration the strong spatial heterogeneity in physical and biological features in the basin.

BIRD DIVERSITY IN LOTIC RIPARIAN ECOSYSTEMS

Key Findings

1. Despite its small area and high elevation, the Lake Tahoe basin exhibited a high richness of 101 bird species of which a large percentage, almost 40%, were aquatic, riparian, or meadow associates. Rare and common species comprised similar proportions of the bird community, with 48% of the species considered rare and 52% considered common.

2. Seven species were both in the top 10 most frequently occurring and most abundant bird species: Steller's Jay, Yellow-rumped Warbler, American Robin, Dark-eyed Junco, Mountain Chickadee, Western Wood-pewee, and Red-breasted Nuthatch.

3. Bird species richness and abundance were highly positively associated. Bird species richness was generally greater in association with a greater amount of meadow and lower precipitation and channel gradient. The richness of all 3 bird habitat groups was also higher in association

with a greater amount of meadow and lower channel gradients. Bird abundance was generally greater in association with a greater amount of meadow, lower elevation, and wider channel width.

4. Bird species richness displayed a potential threshold in association with meadow, where richness was consistently low when meadow comprised < 10% of the sample area, moderate when meadow comprised 10 to 30% of the sample area, and high where meadow comprised > 30% of the sample area.

5. Bird habitat groups exhibited trend relationships with 6 environmental variables. Aquatic species richness was higher, and upland species richness lower in association with (1) decreases in elevation, mixed conifer, and canopy cover and (2) increases in precipitation, lodgepole pine, and channel width.

6. Numerous potential thresholds were observed for the richness of bird habitat groups. Only 1 to 2 aqua-dependent species were observed on reaches over 2200 m, but as many as 7 aqua-dependent species were observed on reaches below 2200 m. The richness of aqua-dependent species was consistently greater where canopy cover index was < 20%. Riparian–meadow-associated species richness was consistently $\geq$ 8 when meadow exceeded 30%, was consistently $\geq$ 6 species when lodgepole pine was present, and was consistently higher on reaches with channel gradients < 10%.

7. All but one of the aqua-dependent species were rare and 60% of the riparian–meadow associates were also rare, whereas only 30% of the upland associates were rare. In addition, only 30% of the rare species were upland associates, whereas 80% of the common species were upland associates.

8. Rare species were more diverse at lower elevation reaches with wide channels, low gradients, and higher sinuosity, as was observed for aqua-dependent species. Rare and common species were both more diverse where there was a greater proportion of meadow and less diverse where there was a greater proportion of subalpine conifer. Rare species richness exhibited negative relationships not observed for common species with aspen–cottonwood, mixed conifer, canopy cover index, and snag and log density.

9. The richness of rare and common species varied by basin orientation in the same manner as aquatic and upland species, respectively, with both groups having high richness on the east side of the basin, and rare species also having higher richness on the south side compared to the north and west.

10. Although reaches ranged widely in environmental conditions, they shared many species, with any given reach containing an average of 35% and as high as 50% of the species observed throughout the basin. Turnover was very low, ranging from only 3 to 7% from the lower to upper ends of the 8 environmental gradients examined. Thus, environmental features that affect alpha diversity (patterns of richness per reach) are the most potent influences on the diversity of birds in the basin.

11. Orographic effects on bird species diversity were substantial. The east and south sides of the basin were associated with significantly greater richness than west and north sides. The east side of the basin appeared to provide an ideal combination of lower elevation, drier areas dominated by upland forest vegetation such as mixed conifer, and a relatively abundant

amount of aspen–cottonwood, such that it supported a diversity of common, upland species. However, rare species, aqua-dependents, and riparian–meadow associates were most diverse on the south side of the basin, where wide streams and lodgepole pine were most prevalent and alder–willow and canopy cover were lowest. Wide streams were not prevalent among the sample reaches, and it is likely that the open stream environments on the south side, and to a lesser extent on the west side of the basin, were among the few areas with suitable habitat for some species, such as Spotted Sandpiper and Canada Goose.

12. The contributions of turnover to the diversity of birds in the Lake Tahoe basin were primarily associated with a few gradients, namely channel flow and orientation, with elevation, aspen–cottonwood and snags and logs invoking more minor levels of turnover. Species turnover along the channel flow gradient was driven by opposing relationships between rare and aqua-dependent species associated with high channel flow and common and upland species associated with low channel flow.

13. Aquatic, riparian, and meadow species restricted to one end of an environmental gradient are potentially more vulnerable to extirpation within the basin. Lazuli Bunting and American Dipper were associated with higher elevation reaches. Many aquatic-, riparian-, and meadow-associated species were restricted to lower elevations; however, Spotted Sandpiper and Tree Swallow were the only frequently occurring species restricted to the lowest elevations. Swainson's Thrush, Winter Wren, and Common Snipe were associated with the moist end of the precipitation gradient. Pine Grosbeak, although not an aquatic, riparian or meadow associate was relatively common and was also absent from the lowest precipitation reaches. Mountain Bluebird was absent from the high flow end of the channel flow gradient. Many aquatic-, riparian-, and meadow-associated species were restricted to higher channel flow, but Spotted Sandpiper was the only frequently occurring species absent from the lowest flow reaches. Swainson's Thrush and Winter Wren were associated with higher snag and log densities, whereas many aquatic, riparian, and meadow species (n = 6) were associated with low snag and log densities. A similar group of 6 aquatic, riparian, and meadow species were associated with the meadow end of the forest to meadow gradient, and no aquatic, riparian, or meadow species were associated with the forest end of the gradient. Swainson's Thrush and Lesser Goldfinch were associated with more subalpine vegetation gradient, whereas Spotted Sandpiper and Mallard were associated with less subalpine vegetation. Swainson's Thrush and Common Snipe were associated with more alder–willow, and Western Meadowlark, Ring-billed Gull, Barn Swallow, and Lesser Goldfinch were associated with less alder–willow. Many aquatic, riparian, and meadow species (n = 8) were associated with more aspen–cottonwood. These species were granivorous and insectivorous ground or aerial foragers, indicating that aspen–cottonwood stands are a rich source of plant and insect food resources.

14. Turnover was high among basin orientations and reflected a combination of range-wide distributional limits and habitat associations. Approximately twice as many species were absent from the north side of the basin compared to any of the other three orientations. Species absent from the east orientation may be limited by xeric conditions or otherwise limited to the Sierra Nevada zoogeographic region. Similarly, species absent from the west orientation may be limited by mesic conditions or otherwise limited to the Great Basin zoogeographic region. For example, the restriction of Winter Wren, Ring-billed Gull, Pine Grosbeak, and Rufous Hummingbird to the west side of the basin may represent the easternmost extension of their ranges at the latitude of the Lake Tahoe basin, given that they were absent from the east side of the basin and do not occur in Nevada. Swainson's Thrush

range extends east of the basin into Nevada, so the apparent restriction of this species to cooler, wetter west orientation reflects habitat associations versus distributional limits. Common Raven, Northern Pygmy Owl, and Turkey Vulture were only found on the warmer, drier orientations in the Lake Tahoe basin, and since they are widely distributed in California and Nevada, their distribution in the basin probably reflects habitat associations.

15. The forest to meadow gradient had the greatest contribution to overall diversity in the basin, exhibiting a shift of 39 species along its gradient, almost 40% of the total bird fauna. The forest to meadow gradient was followed by elevation, aspen–cottonwood, and snag and log gradients. The difference in compositional change among the gradients ranged as high as 21 species—over 20% of the observed total species richness—with all gradients differing by a maximum of 10 species (approximately 10% of the bird fauna).

16. Vegetation had the greatest influence on bird species richness and abundance in the Lake Tahoe basin, whereas channel flow and elevation factors had the greatest influence on species composition. The diversity of vegetation types at low to mid elevations, namely meadow, lodgepole pine, alder–willow, and aspen–cottonwood, is largely responsible for the relatively high species richness observed in the basin compared to similar environments studied by others. The steep elevation, precipitation, geomorphological, and orographic gradients also create a diversity of environments. Additionally, the Lake Tahoe basin also lies along a major east–west division between biogeographic zones providing an enhanced assemblage of species. The combination of these varied conditions is the key progenitor of high bird diversity in the riparian areas in the basin.

Management Recommendations

1. The majority of birds found riparian environments to be suitable throughout a large proportion of the Lake Tahoe basin, as evidenced by high alpha diversity. This pattern suggests that conservation strategies for birds could have a great deal of flexibility to accommodate other conservation or development considerations. The identification of areas with the highest diversity of bird species, particularly less common species, would be an important step. However, once identified, the location of additional sites with an emphasis on maintaining and conserving biological diversity could be flexible. The applicability of a combination coarse- and fine-filter approach for the purposes of conserving bird diversity in the Lake Tahoe basin is discussed below.

2. Higher species richness at low elevations combined with unique species occurring at higher elevations makes for a demanding conservation scenario, given that lower elevation environments are most vulnerable to human disturbance in the basin. A conservation strategy for the biological diversity of birds would be most effective if efforts were concentrated at lower elevation sites and encompassed as broad a diversity of vegetation types and aquatic environments as possible, since gains in bird diversity will be incremental and will generally track the diversity of environments.

3. The management of meadows, particularly those at mid to low elevations, could have significant effects on the richness of aquatic-, riparian-, and meadow-associated birds. The greatest threats to meadow condition and extent are lack of fire, which can affect succession, and water diversions and grazing, which can affect the hydrodynamics of meadows. Prescribed fires and wildfires that are allowed to burn should generally improve the quality and quantity of meadows in the basin. Channel restoration efforts should consider potential impacts on meadow systems. Most meadows in the basin are currently grazed by cattle, and

grazing can have a deleterious effect on many bird species, particularly ground and shrub nesting aquatic, riparian, and meadow associated species.

4. Lodgepole pine stands, particularly in association with meadows, played an important role in supporting high species richness at lower elevations. Any effort to conserve the richness and diversity of aquatic, riparian, and meadow bird species in the Lake Tahoe basin would benefit from special management considerations for lodgepole pine in proximity to streams and meadows. Potential management impacts include cattle grazing and fire management.

5. Alder–willow provided valuable habitat for riparian–meadow-associated bird species, as well as supporting common species. Grazing, channel restoration, and beaver could alter its distribution and abundance. Restoration efforts that involve key meadow complexes with well developed alder and willow vegetation should be carefully considered so as to avoid detrimental effects on riparian and meadow bird habitat.

6. Aspen–cottonwood had a strong influence on bird diversity through a combined influence on richness and turnover. The relatively high diversity associated with aspen–cottonwood in spite of its infrequent occurrence on sample reaches suggests that aspen and cottonwood may function as keystone species relative to bird diversity in the Lake Tahoe basin. Given the substantial contribution of aspen and cottonwood to bird diversity in the Lake Tahoe basin, it would be ideal to manage aspen for its wildlife values. Larger stands of aspen and cottonwood may provide particularly valuable habitat for a wide array of species, given that other studies have found that stand size can significantly affect the richness and abundance of associated birds. The increased use of prescribed fire and proportion of wildfires that are allowed to burn are likely to improve the vigor and perhaps the extent of aspen stands in the basin.

7. Management of snags and logs to benefit bird diversity should focus on the retention and recruitment of large snags and logs. Attempts to reduce fine fuels in the Lake Tahoe basin may reduce the density of small snags and logs, but may also pose a risk to the quality and quantity of large snags and logs. Careful fire management to conserve values provided by large snags and logs would contribute to retaining valuable habitat elements for many bird species.

8. The concept of a coarse-filter approach to conservation, developed by the Nature Conservancy, would apply well in the case of conserving the majority of stream-associated bird species in the Lake Tahoe basin. The coarse-filter approach would entail conserving a breadth of vegetation and aquatic community types without specific attention paid to the species associated with each. Fine-filter conservation approaches consider additional environmental requirements for species that are not supported by a coarse-filter approach, such as species that are specialists, rare, geographically restricted, or declining in numbers.

9. The individual species identified as potential specialists, as well as species considered rare or limited to 1 to 2 basin orientations, are good candidates for fine-filter conservation considerations. Seven species were detected at $\geq$ 10% of the reaches and were restricted in their occurrence along one or more gradients suggesting specific bounds in the extent of their niches in the basin: Spotted Sandpiper, Mallard, Spotted Towhee, Tree Swallow, American Dipper, White-crowned Sparrow, and Black-headed Grosbeak. These species, although frequently occurring, may be particularly susceptible to environmental changes, and should be considered specifically in riparian management.

MAMMAL DIVERSITY IN LOTIC RIPARIAN ECOSYSTEMS

Key Findings

1. I encountered a high richness of 35 species of mammals, of which approximately 35% were aquatic, riparian, or meadow associates. Rare and common species comprised similar proportions of the mammal community, with 46% considered rare and 54% considered common.

2. Seven species were both in the top 10 most frequently occurring and most abundant mammal species: deer mouse, long-tailed vole, long-eared chipmunk, golden-mantled ground squirrel, yellow-pine chipmunk, Trowbridge's shrew, and western jumping mouse.

3. Although reaches ranged widely in environmental conditions, they shared many species, with any given reach containing an average of 26% and as high as 49% of the total number of mammal species observed throughout the Lake Tahoe basin. Concomitantly, turnover was relatively low, ranging from 6 to 14% from the lower to upper ends of the 8 environmental gradients examined. Therefore, environmental features that affect alpha diversity (patterns of richness per reach) and rare species are the most potent influences on the diversity of mammals in the Lake Tahoe basin.

4. Aspen–cottonwood, lodgepole pine, and elevation were the environmental features most strongly associated with the higher richness of mammals. Aspen–cottonwood and lodgepole pine supported more rare species, whereas upper elevations supported more common species. All measures of richness, with the exception of common species richness, increased with increases in aspen–cottonwood, and at least 6 mammal species were observed wherever aspen–cottonwood occurred.

5. Lodgepole pine, the other environmental feature associated with higher richness of rare species, rarely (n = 3 reaches) co-occurred with aspen–cottonwood. Thus, at upper elevations where lodgepole pine was more common than aspen–cottonwood, rare species were richest in association with lodgepole pine.

6. Total richness and the richness of common species increased with elevation. Above 2500 m in elevation, $\geq$ 5 mammal species were consistently observed per reach. Although richness generally increased with elevation, the number of species per elevation segment (n = 20 reaches) did not vary substantively among segments from low to high elevation. Increases in richness associated with elevation reflected a slightly greater richness of species occurring at higher elevations combined with an increased frequency of occurrence per species on higher elevation reaches. Thus, mammal species were more ubiquitous at higher elevations.

7. Both habitat groups (aquatic–riparian–meadow- and upland-associated species) were highly related to environmental conditions described in this study. This suggests that many upland mammal species use riparian environments for some aspect of their life history (e.g., cover, feeding, resting, reproduction, thermoregulation).

8. Three environmental variables strongly differentiated the richness of aquatic–riparian–meadow associates from that of upland associates: channel gradient, meadow, and canopy cover index. Aquatic–riparian–meadow associates were most speciose in association with high channel flow conditions and open, meadow environments, with

mountain pocket gopher, long-tailed vole, and montane vole being among the most frequently occurring aquatic–riparian–meadow-associated species. Conversely, upland associates were most speciose in association with low channel flow conditions and forested environments.

9. Analysis of species groups revealed that the primary vegetation gradient (forest to meadow) supported a mammalian gradient (aquatic–riparian–upland species), and that meadow and lodgepole pine habitats provided habitat for a large proportion (60% of the mammal assemblage was rare) of the mammalian fauna in the Lake Tahoe basin.

10. The richness of common species was closely correlated with abiotic conditions, increasing with lower channel flows, upper elevations, and a lower abundance of meadow, with deer mouse, long-eared chipmunk, Douglas squirrel, and California ground squirrel being the most frequently occurring upland-associated species.

11. The greatest contribution of turnover to the diversity of mammals in the Lake Tahoe basin was associated with alder–willow and elevation. The alder–willow gradient was ranked the highest contributor to species turnover, with a total turnover of 12 species. It also had the highest average Whittaker's beta diversity index. Rare species were primarily responsible for the high turnover along the alder–willow gradient. High turnover of rare species, combined with a slight decline in species richness resulted in alder–willow having a major effect on the composition of mammals in the Lake Tahoe basin.

12. Elevation was unique in its association with both richness and turnover. A high proportion (25%) of all mammal species occurring on more than one reach were restricted to lower or higher elevation reaches. Although many high elevation associates were common, habitat specialists such as shadow chipmunk and ermine were also associated with higher elevations.

13. Orographic effects on mammal species were substantial, given that mammal richness varied significantly and turnover was high among basin orientations. The geographic location and topographic configuration of the Lake Tahoe basin converge to create a unique faunal interchange between zoogeographic regions, which is reflected in the distribution of mammal species in the basin. These influences were expressed in the difference in species composition observed between the north and east orientations and south and west orientations. All measures of diversity varied by orientation, with the exception of rare species richness and total abundance. The east side of the basin, and the north side to a lesser extent, supported a high richness of common and upland mammal species by providing a highly suitable combination of lower elevation, drier areas dominated by upland forest vegetation, such as mixed conifer, and a relative abundance of aspen–cottonwood. Most of the 7 species restricted to the north or east side of the basin are associated with drier environments. In contrast, aquatic–riparian–meadow species were most speciose in association with the more mesic conditions on the west side of the basin.

14. The channel flow and alder–willow gradients had the greatest contribution to gamma diversity in the basin, exhibiting shifts of 16 and 15 species (respectively) comprising approximately 43% of the total mammal fauna. Changes in species composition were greater at the lower end of the channel flow gradient, being driven at least in part by opposing relationships between upland species (associated with low channel flow), and aquatic–riparian–meadow species (associated with high channel flow). The shift toward aquatic–riparian–meadow species in association with higher channel flow was accompanied by a loss in species richness. The diversity associated with the alder–willow gradient was

primarily driven by species turnover, whereas a greater balance of shifts in richness and turnover were associated with the channel flow gradient.

15. A number of species exhibited limits in regard to one or more environmental gradients, including the alder–willow, elevation, subalpine vegetation, and snag and log gradients. The greatest number of species was absent from some portion of the alder–willow gradient, including raccoon, porcupine, hares, and mountain pocket gopher. The raccoon and porcupine were present only in areas with a low proportion of alder–willow. At the other end of the gradient, the occurrence of hares where alder–willow was more abundant is indicative of a habitat specialization. Finally, the abundance of mountain pocket gopher increased with alder–willow, indicating favorable soil characteristics or perhaps food resources in the form of roots of alder–willow or associated plant species. Four mammal species exhibited limits along the elevation and subalpine vegetation gradients: ermine, gray squirrel, raccoon, and coyote. The ermine and was absent from the lowest elevation reaches. The higher elevation occurrence of ermine could be the result of competitive exclusion induced by its larger congener, the long-tailed weasel. The gray squirrel and raccoon were absent from higher elevations, and the coyote and gray squirrel were similarly absent from the upper most segment of the subalpine vegetation gradient. Gray squirrel and raccoon are above their typical elevational limit in the Lake Tahoe basin, and appear to be restricted to the lower elevations (and associated vegetation types) in the basin. The coyote is a common species in the Lake Tahoe basin and a habitat generalist, but food resources may be more limited at higher elevations and winter movement more difficult where snow packs are deeper. The long-tailed weasel was absent from reaches with the highest densities of snags and logs. The long-tailed weasel is known to forage in more open habitats, and preys primarily on voles and mice, as well as chipmunks, gophers, and squirrels.

Management Recommendations

1. Sierra Nevada-associated species such as long-eared chipmunk, bushy-tailed woodrat, Douglas squirrel, and mountain pocket gopher were found on the Nevada (east) side of the basin along with desert-associated species, such as least chipmunk, Nuttall's cottontail, and desert woodrat. In the Lake Tahoe basin, almost half of the mammal species are at the east–west edge of their range, and persistence of their populations is critical to maintaining mammal diversity in the basin.

2. The greater frequency of occurrence of species at higher elevations, in association with no substantive change in the number of unique species, could be explained by a combination of a few phenomenological influences. Environmental homogeneity is likely to be partially responsible for the observed patterns of richness, yet it does not explain why the number of unique species did not decline with elevation. The topographic isolation of the Lake Tahoe basin could be effecting a reduced richness of mammal species at lower elevations, particularly along the higher Sierra crest which defines the western boundary of the basin. Fauna at the lowest elevations in the basin would normally be enriched by species associated with even lower elevations. However, the Lake Tahoe basin is surrounded by mountain crests, with only a few topographic saddles as low as 2100 m. Species that could persist at lower elevations within the basin may be absent because topographic barriers prevent these species from immigrating into the basin or suitable habitat is too limited to support populations once they arrive. Further experimental studies are needed to confirm this hypothesis.

3. Human disturbance within the Lake Tahoe basin is substantial, and it is greater at lower elevations, in proximity to Lake Tahoe. Human disturbance includes conversion of natural environments to buildings and parking lots, fragmentation of natural environments by roads and rural communities, direct human disturbance from hikers, bikers, and motorized vehicles, and disturbance from livestock grazing. The protection of riparian environments from degradation and facilitating the ability of populations to reestablish if local extirpations were to occur are important conservation considerations in planning and managing for mammal diversity in lotic riparian environments in the basin.

4. Alder–willow contributed substantially to supporting mammal diversity. A range of densities of alder–willow may increase the spatial heterogeneity of resources across reaches thereby providing habitat for a greater number of species. Alder and willow occurred frequently along stream reaches, and were generally well-distributed throughout the Lake Tahoe basin. Management activities are unlikely to change the distribution of alder and willow, but grazing and channel restoration could alter its abundance. Channel restoration could restore alder-willow vegetation where it has known to be reduced or lost, but it could also negatively affect the distribution and abundance of alder and willow. Restoration efforts in areas with well-developed alder and willow vegetation should be carefully considered so as to avoid detrimental effects on riparian and meadow environments.

5. The management of meadows and mixed conifer forests at mid to low elevations could have significant effects on the richness of aquatic, riparian, and meadow associated mammals. The greatest potential impacts to mixed conifer forests are the lack or mismanagement of fire (prescribed and wildfire), timber harvest, and recreation disturbance. The greatest threats to meadow condition and extent are lack of fire, which can affect succession, and water diversions and grazing, which can affect the hydrodynamics of meadows (Ratliff 1985). Prescribed fires and wildfires that are allowed to burn, and timber harvested with the intent of mimicking natural processes (e.g., fire, disease, windthrow), should generally improve the quality and quantity of vegetative conditions in the basin. Channel restoration efforts should consider potential impacts on meadow systems.

6. Lodgepole pine plays an important role in supporting mammal diversity, particularly in supporting rare species. Any effort to conserve the richness and diversity of aquatic, riparian, and meadow mammal species in the Lake Tahoe basin would benefit from special management considerations for lodgepole pine in proximity to streams and meadows. Potential management impacts include cattle grazing and fire management.

7. Woody debris can be a benefit or a detriment to mammal diversity in the Lake Tahoe basin, depending on its dimensions and abundance. Management of woody debris to benefit mammal diversity should focus on the retention and recruitment of large logs. Attempts to reduce fine fuels in the Lake Tahoe basin may reduce the density of small snags and logs, but may also pose a risk to the quality and quantity of large snags and logs. Charring may reduce the suitability of snags and logs for wildlife species. The management of forests through timber harvest, fuelwood harvest, and fire should consider their impact on log quantity and quality for the benefit of mammal diversity.

8. The fact that aspen–cottonwood was so strongly associated with mammal richness despite its rarity in the Lake Tahoe basin suggests that this vegetation type serves a pivotal role in supporting mammal diversity. The highest densities of rodents in aspen stand tend to occur in mature stands. Mammal species detected in this study expected to be closely associated with

aspen–cottonwood include mountain pocket gopher, porcupine, black bear, mule deer, and deer mouse. Aspen and cottonwood provide the greatest opportunity of any riparian woodland vegetation type for enhancing habitat values for riparian-associated mammal species in the Lake Tahoe basin. It is possible that the lack of fire has reduced the extent of aspen in the basin. The increased use of prescribed fire and proportion of wildfires that are allowed to burn are likely to improve the vigor and perhaps the extent of aspen stands in the basin.

9. The concept of a coarse-filter approach to conservation, developed by the Nature Conservancy, would apply well in the case of conserving the majority of mammal species associated with lotic riparian environments in the Lake Tahoe basin. The coarse-filter approach would entail conserving a breadth of vegetation and aquatic community types without specific attention paid to the species associated with each. Fine-filter conservation approaches consider additional environmental requirements for species that are not supported by a coarse-filter approach, such as species that are specialists, rare, geographically restricted, or declining in numbers.

10. The individual species identified as potential specialists, as well as species considered rare, or limited to 1 to 2 basin orientations, are good candidates for individual conservation considerations. For example, east orientations appears to offer the only suitable habitat for some Great Basin associated species. The location, distribution, and timing of conservation actions (e.g., water development projects, control of exotics) and management treatments (e.g., prescribed fire, timber harvest, road building) should take into consideration the potential impacts on geographically limited species. Species known to be declining in numbers were not specifically addressed in this study, but obviously they should also be included in the development of any fine-filter conservation approach.

11. This study results suggest that survey or monitoring efforts need to analyze patterns in richness and composition at more than one spatial scale to obtain an accurate depiction of relationships between diversity and environmental gradients.

INVERTEBRATE DIVERSITY IN LOTIC RIPARIAN ECOSYSTEMS

Key Findings

1. Approximately one half of the 500 insect families occurring in California, a total of 254 families, were detected during sampling. Only 20% of the families encountered were considered aquatic or semi-aquatic, with the remainder considered terrestrial. Aquatic and semi-aquatic families generally had lower frequency of occurrence compared to terrestrial families. Over 60% of the invertebrate families were considered rare (frequency of occurrence < 25%).

2. The number of families shared among reaches was low, with an average of 25% (ranging from 15% to 40%) of all families occurring at any given reach. Alternatively, turnover averaged 12% from lower to the upper half of the 8 environmental gradients examined. Therefore, richness and turnover both contributed substantially to the diversity of invertebrate families, and environmental features that affected alpha and beta diversity all influenced the diversity of invertebrates in the Lake Tahoe basin.

3. Taxonomic richness and invertebrate family richness were highly correlated. The 10 most frequently occurring families consisted of a wide range of taxonomic groups and accounted

for less than 20% of all observations. Family richness was positively associated with lodgepole pine, alder–willow and meadow, and negatively associated with channel gradient.

4. Meadow, although occurring on less than half of the sample reaches, had a strong influence on invertebrate richness of all environmental features assessed. Invertebrate family richness increased from a low of 25 families where meadow occupied $\leq$ 10% of the reach to at least 50 families where meadow occupied $\geq$ 30% of the reach. Approximately 40 more families were associated with reaches with an abundance of meadow and lodgepole pine compared to reaches with an abundance of mixed conifer.

5. The amount of alder–willow occurring on a given reach considerably affected the composition of invertebrate families. And although many measures of invertebrate richness (i.e., total richness, semi-aquatic, and terrestrial groups) increased with increases in alder–willow, the number of families gained along the alder–willow gradient was relatively low (average of 12 families gained per segment). This apparent contradiction was the result of a greater frequency of occurrence per family associated with upper segments of the alder–willow gradient. These results suggest that alder–willow provides a set of unique physical structures and an array of resources, but homogeneous environment, that provides habitat for a unique assemblage of families.

6. Lepidoptera genus richness was positively correlated with many other richness measures (total family richness, common family richness, and terrestrial family richness), but virtually no relationships were observed between the richness of Lepidoptera genera and the environmental features described in this study.

7. Invertebrate richness increased with increases in aspen–cottonwood, particularly the richness of rare families. Aspen–cottonwood provides a rich array of resources and supports a unique array of invertebrate families.

8. Associations of total richness were driven largely by common and terrestrial families, with the associations of rare and aquatic families not strongly expressed in this composite measure.

9. Aquatic and terrestrial family groups were both positively correlated with channel flow, but otherwise shared few associations. Aquatic family richness was governed more by abiotic conditions (higher richness associated with low elevation and high precipitation) and was uniquely associated with channel width. At least 2 aquatic families were present where average annual precipitation exceeded 110 cm. In contrast, semi-aquatic and terrestrial family richness were governed more by vegetative conditions (higher richness associated with riparian and meadow vegetation). As with invertebrate family richness, at least 50 families of terrestrial families were present where meadow exceeded 30%.

10. The richness of rare families was higher in association with meadows, and was likely to be largely responsible for the positive association between invertebrate richness and meadows, and the negative association between invertebrate richness and snags and logs. The richness of common families was higher in association with alder–willow vegetation and low gradient, slow flowing streams.

11. Channel flow was the most influential non-biotic environmental feature associated with invertebrate family richness. Richness, as reflected in many measures (total richness, richness of both frequency classes, aquatic and terrestrial group richness), increased with channel flow.

12. Total richness did not vary significantly by orientation, but aquatic family richness was higher on more mesic south and west sides compared to the north and east sides of the basin. Of the vegetative features most associated with invertebrate richness (meadow, alder–willow, and lodgepole pine), only lodgepole pine varied by orientation. Physical characteristics also varied considerably among orientations, with precipitation and channel width varying most significantly. The large numbers of families absent from one or more orientations far exceeded the number observed for any of the environmental gradient segments. Of the 15 families with frequencies $\geq$ 10% that were absent from one or more orientations, 4 were aquatic: Heptageniidae (stream mayflies; missing from the west side), Perlodidae (common stoneflies; missing from east and south sides), Corixidae (water boatmen; missing from the north side), and Coenagrionidae (narrow-winged damselflies; missing from the north side). Only one family with a frequency $\geq$10% was missing from $\geq$ 2 orientations; Perlodidae (n = 7) (common stoneflies of the Plecoptera order) was missing from east and south sides of the basin. Perlodidae are common in cool, clear streams, and the north and west sides of the basin had the highest elevation stream reaches in the study area. It is possible that stream temperature had some part to play in the distribution of Perlodidae.

13. Alder–willow had the highest beta diversity, followed by channel flow and precipitation. Total turnover was 81 families along the alder–willow gradient, with a core turnover of 22 families. Channel flow had a total turnover of 78 families, with a core turnover of 27 families.

14. The alder–willow gradient had the greatest number of frequently occurring families restricted to one portion of its length compared to the other environmental gradients. Seven families with frequencies $\geq$ 10% were absent at one or the other end of the alder–willow gradient: Geometridae, Acroceridae, Therevidae, Hemerobiidae, Pompilidae, Sarcophagidae, and Largidae. Geometridae and Acroceridae were absent from reaches with the greatest amount of alder–willow. Five families were absent from reaches with the least alder–willow: Therevidae (stiletto flies), Hemerobiidae, Pompilidae, Sarcophagidae (flesh flies), and Largidae (largid bugs). These families may be dependent on alder-willow.

15. The highest number of families with $\geq$10% frequency (n = 10) were restricted to meadow environments, as evidenced by high turnover along the forest to meadow gradient. Further, many of these families (n = 5) did not show restrictions along any other gradient. Four of these 5 families were in the Diptera order, consisting of various types of flies, including Ephydridae, which are shore flies associated with moist environments. The fifth was an aquatic family, Corixidae (water boatmen). It is clear that although the forest to meadow gradient had the lowest beta diversity, there are a relatively high number of families, primarily Dipterans, uniquely associated with dry and moist meadow environments.

16. Vegetation was the greatest contributor to the overall diversity of invertebrate families, with meadow, lodgepole pine, alder–willow, and aspen–cottonwood being the top 4 contributors. Despite the steep elevation and precipitation gradients in the Lake Tahoe basin, these variables had limited association with invertebrate family diversity, where only aquatic family richness increased with precipitation and decreased with elevation. Channel flow also had a positive influence on invertebrate richness, but turnover was low.

17. Riparian woodland vegetation (i.e., alder–willow and aspen–cottonwood), in conjunction with meadow, comprised the trio of vegetation types that contributed the most to the diversity of invertebrate families. Richness and turnover had opposing patterns of association with all

gradients, and in relation to these top 3 environmental gradients, richness decreased and turnover increased from forest to meadow and with increases in aspen–cottonwood and alder–willow.

Management Recommendations

1. Meadows occupied the highest percentage of each reach where channel flow was lowest and the proportion of meadow occupying each reach increased with decreases in channel gradient. These relationships suggest that low gradient channels are associated with more open-canopied environments and they have greater access to floodplains, which in turn increases stream productivity and the development of riparian-associated vegetation.

2. The high diversity of invertebrate families, their close association with vegetation, and the dual contributions of richness and turnover indicates that the quality and diversity of vegetative conditions would be critical to the conservation of invertebrates. Conservation of invertebrate diversity would require areas large enough to support the richness of the site, and many sites such that representatives were identified for the full diversity of vegetation types, emphasizing meadow and riparian woodland vegetation types and lower elevation areas.

3. The strong role of vegetation types in my study, particularly meadow and riparian woodland types, in supporting a diversity of invertebrates in the Lake Tahoe basin has important management implications. Most importantly, the management of meadow and riparian vegetation supports not only aquatic and semi-aquatic invertebrates, but a wide range of terrestrial families as well. Channel restoration projects can potentially have the greatest influence on these vegetative conditions, and their impacts on riparian and meadow vegetation should be considered in light of their importance to invertebrate diversity.

4. Meadows and grasslands are considered highly productive environments and are commonly associated with rich invertebrate assemblages. Based on the results of this study, meadows may serve an important role in the support of invertebrate diversity in the Lake Tahoe basin. The presence of some meadow appears to greatly enhance the richness of invertebrate families, and thus meadow management should be a primary element in any strategy for the conservation of invertebrate diversity in the basin. Conversely, invertebrate diversity should be considered in the management of meadows.

5. Thresholds observed for invertebrate family richness in relation to the amount of meadow corroborate the results of other studies showing that resources associated with meadows (e.g., food, cover, nest sites) may reach necessary levels of abundance or diversity only in meadows above a certain size or extent. The greatest threats to meadow condition and extent are lack of fire, which can affect succession, and water diversions and grazing, which can affect the hydrodynamics and plant diversity of meadows. Prescribed fires and wildfires that are allowed to burn should generally improve the plant diversity and extent of meadows in the basin. Channel restoration efforts should consider potential impacts on meadow systems. Most meadows in the basin are currently grazed by cattle, and only a few allotments exclude cattle from grazing adjacent to stream channels. Grazing may have a deleterious effect on plant species composition, diversity, and flower production if over-grazed.

6. It appears that aspen–cottonwood provides unique resources (type, quality, or quantity) which contribute substantially to the richness of invertebrates in the Lake Tahoe basin and provide habitat for less frequently observed families which may be rare in the basin. Given that

aspen–cottonwood represented a relatively weak vegetation gradient, its strong association with diversity suggests that it may function as a sort of "keystone" resource for the gamma diversity of invertebrates in much the same manner as that discussed for bird diversity in lotic ecosystems. As such, it would be ideal to manage aspen for biological diversity. In the Lake Tahoe basin, it is possible that the lack of fire has reduced the extent of aspen. The increased use of prescribed fire and proportion of wildfires that are allowed to burn are likely to improve the vigor and perhaps the extent of aspen stands in the basin.

7. Given the high richness and turnover associated with alder and willow vegetation, a range of densities of alder and willow would probably provide habitat for a the greatest number of families. Management activities are unlikely to change the distribution of alder and willow, but grazing and channel restoration could alter its abundance. In particular, channel restoration could affect alder and willow abundance, as well as meadow conditions. Restoration efforts that involve key meadow complexes with well developed alder and willow vegetation should be carefully considered so as to avoid detrimental effects on riparian and meadow vegetation and habitats for invertebrates.

8. The snag and log gradient was negatively associated with invertebrate family richness, a relationship that was driven primarily by terrestrial and rare families. It is likely that the negative association of invertebrate richness with snags and logs is an indirect reflection of the strong positive association between richness and meadows. Woody debris is an important substrate and food source for many invertebrate taxa, including the 7 families restricted to the upper end of the snag and log gradient. These 7 families could be greatly affected by forest management that greatly reduces snag and log densities. Attempts to reduce fine fuels in the basin may reduce the density of small snags and logs, but may also pose a risk to the quality and quantity of large snags and logs. Charring can reduce the suitability of snags and logs as foraging substrates or cover for invertebrates. Careful fire management to conserve the quality and quantity of large snags and logs would contribute to retaining valuable habitat elements for forest-associated invertebrates.

9. The positive effect of channel flow on invertebrate diversity and the relatively high turnover along the channel flow gradient points toward careful consideration of invertebrates in the management and restoration of stream channels in the Lake Tahoe basin. Only aquatic family richness increased in concert with channel width, and thus low-gradient, wide channels may provide special habitats and conditions for aquatic invertebrates which facilitate their higher richness. The assemblages of families associated with wide streams and their environmental requirements and sensitivities should be considered in restoration activities regardless of their location in a watershed.

10. In this study, elevation and precipitation had a minor influence on the richness of invertebrate families, but they did affect aquatic invertebrate richness. Although forest management does not affect elevation and precipitation, it is important to note that the richness of aquatic invertebrates will be more greatly affected at lower elevation sites, particularly in areas of higher precipitation such as the west side of the basin.

11. Strong environmental relationships were observed for invertebrate family richness. This suggests that the resolution of diversity and environmental variables were compatible. My results indicate that addressing diversity at the family level could be a tenable option for monitoring invertebrate diversity at geographic scales as large or larger than the Lake Tahoe basin (> 100,000 ha).

12. The inverse relationship observed between alpha and beta diversity is probably a function of assessing invertebrate richness at the family level. Most invertebrate families (particularly the terrestrial ones) encompass a high number of species with varying habitat associations. It is likely that turnover in species composition along these gradients is high, because as richness increases, the probability of the same family occurring in opposing biotopes or habitat conditions would be greater than for the same genus or species. Studying patterns of invertebrate richness at a variety of taxonomic levels, including family, genus, and species levels, would provide more ecologically-based relationships between alpha and beta diversity by revealing the differential rate of turnover among taxonomic levels. Once established, shifts in higher taxonomic levels along key environmental gradients may serve as strong indicators of lower level shifts in richness and composition.

13. The inclusion of spider families in the calculation of invertebrate richness greatly broadened the phylogenetic diversity of invertebrate taxa. Increasingly, spiders are being considered for use as indicator taxa as measures of diversity and indicators of environmental conditions. Although a high level of expertise is needed to identify spider species, the use of morphospecies as a metric of richness has promise as a strong indicator of the biological diversity of spiders.

14. Butterflies have been suggested as potential indicators of the diversity of other taxa, including other invertebrates and vertebrates. The lack of associations observed between Lepidoptera genus richness and environmental features may be a function of assessing them at the genus level. The potential of Lepidoptera species or genera to serve as indicators of environmental conditions warrants further investigation.

VASCULAR PLANT DIVERSITY IN LOTIC RIPARIAN ECOSYSTEMS

Key Findings

1. I encountered a high number of plant species (n = 470), comprising approximately 44% of all plant species known to occur in the Lake Tahoe basin. Only 45% of all plant species detected were considered aquatic, riparian, meadow associates. Further, the equivalent strength of the correlation of aquatic–riparian–meadow and upland species richness with total species richness indicates that riparian-associated vegetation was often less than 30 m in width, and upland-associated plant species commonly occurred within 30 m of stream channels.

2. The number of plant species shared among reaches was low, with an average of only 15% of all species occurring on any given reach. Similarly, turnover averaged 16% from lower to upper half of the 8 environmental gradients examined. Therefore, richness and turnover both contributed substantially to the diversity of plant species. Several environmental features were associated with each measure of plant species diversity.

3. Plant species richness was higher in response to increased moisture as represented by increases in association with higher precipitation, west aspects, and greater channel widths. Precipitation was also positively associated with aquatic–riparian–meadow species richness and the richness of both rare and common plant species. This suggests that it affects all plant species in a similar manner, but the lack of relationship with upland species suggests that it affects upland species to a lesser degree than species more closely associated with mesic environments.

4. Precipitation and richness had a marked curvilinear relationship, expressed in total plant species richness, as well as aquatic–riparian–meadow species richness, and common species richness. Average annual precipitation ranged from 50 to 203 cm, and richness peaked at intermediate levels of 110 and 130 cm per year. Such a curvilinear relationship could be interpreted as reflecting the “paradox of enrichment” response. However in the Lake Tahoe basin, high precipitation coincides with high elevation, negating some of the potential gain in productivity that may have accompanied increased precipitation. Higher richness associated with the mesic, west side of the basin versus lower richness associated with the xeric, east side of the basin provides further evidence that moisture is a primary limiting factor for plant species richness. The more mesic west and north sides also had the greatest number of unique species (high beta diversity), most of which were rare (i.e., low frequency of occurrence).

5. Four vegetation types were associated with plant species richness: lodgepole pine, subalpine conifer, aspen-cottonwood and meadow. Richness was greater in association with all of these vegetation types except meadow. Lodgepole pine, like precipitation, was also associated with higher richness of aquatic–riparian–meadow species, and both rare and common species. Thus, precipitation and lodgepole pine appeared to have the greatest overall association with plant species richness.

6. Potential thresholds in plant species richness were observed in relation to the amount of lodgepole pine. Where lodgepole pine was > 10% of the reach, plant species richness was consistently ≥ 50 species. Further, plant species richness appeared to peak when lodgepole pine occupied approximately 40% of the reach, and then declined slightly with greater proportions of lodgepole pine.

7. Aspen–cottonwood was positively associated with plant species richness and aquatic–riparian–meadow richness in particular. Plan species richness was consistently > 60 species when at least 10% of the reach was occupied by aspen-cottonwood, whereas it dropped to as low as 30 species with at lower proportions. Aspen–cottonwood is known for its high species richness, which is attributed to its affiliation with moist environments. It provides a uniquely rich environment at the intermediate elevations where it occurs in the Lake Tahoe basin.

8. Alder–willow was also positively associated with the richness of aquatic–riparian–meadow species. Alder–willow vegetation is the predominant woody component of the montane riparian vegetation in the Lake Tahoe basin, and it occurred frequently (over 95% of all sample reaches) but typically occupied a small proportion of a reach (average < 20%). Alder–willow is typically a compositionally simple vegetation type, suggesting that it is the associated moisture regime that supports a rich plant community as opposed to reflecting the richness of the alder–willow community itself.

9. Aquatic–riparian–meadow and upland associates had opposing relationships with channel gradient and mixed conifer. Aquatic–riparian–meadow richness was greater in association with wide, low gradient streams, whereas common species decreased in richness in association with these same channel flow characteristics. The 2 groups also had opposing relationships with forest to meadow gradient and mixed conifer (which represented the forest end of the forest to meadow gradient), with aquatic–riparian–meadow species richness being greater in association with the meadow end of the gradient.

10. Rare and common species had very different environmental associations. Rare species richness was positively associated with lodgepole pine and meadow and higher channel flows, whereas common species richness was positively associated with woody vegetation (conifer forests and alder–willow) and lower channel flows. These patterns of association are consistent with those observed for aquatic–riparian–meadow and upland species richness, respectively.

11. Based on high correlations between rare and aquatic–riparian–meadow, as well as between common and upland species, it is clear that aquatic–riparian–meadow species were relatively rare compared to upland species. Indeed, 3 of the 6 most common species were dominant woody species, including white alder, white fir, and Jeffrey pine.

12. Turnover was highest in association with the elevation gradient, along which temperature, length of growing season, and atmospheric moisture are known to vary. A total of 213 species, almost 50% of all species encountered, turned over along this gradient. It was apparent that turnover was higher between and within lower elevation segments compared to higher elevation gradients. The number of core turnovers along the elevation gradient was second only to precipitation, indicating that elevation had a fundamental influence on the composition of plant species.

13. The snags and log gradient had the second highest turnover, with a total turnover of 200 species and a core turnover of 75 species. Turnover was higher at the lower end of the snag and log gradient suggesting that greater heterogeneity of environments existed where woody debris, particularly logs, was less abundant. High turnover is also likely to be the result of the bimodal relationship observed for richness along the snag and log gradient, where richness was high in the lowest end of the gradient (probably meadow environments) and high again in the second highest segment of the gradient where snag and log densities in forested environments appeared to reach some optimum level for many plant species.

14. The channel flow gradient had the third highest turnover, with a total turnover of 198 species and a core turnover of 90 species. The influence of channel flow on turnover is strongly related to the diversity patterns observed in association with the forest to meadow gradient. As observed with the forest to meadow gradient, species richness per reach did not vary significantly because species had a lower frequency of occurrence on reaches with high channel flow characteristics. Thus, low gradient, wide channels were associated with a rich and heterogeneous environment that provided for relatively high diversity of plant species, particularly aquatic, riparian, and meadow associates.

15. The forest to meadow gradient ranked the highest overall in its contribution to diversity, showing a shift of close to 60% of the plant flora. The forest to meadow gradient was not associated with particularly high richness or turnover. Rather, it was a major contributor to diversity through the combined contributions of richness and turnover. Although increases in richness were observed from low to high segments of the forest to meadow gradient, I did not observe a correlation between plant species richness and the forest to meadow gradient. Upon closer examination, it was apparent that the average frequency of occurrence of plant species decreased from forests to meadows. Thus, although the number of species per reach was not greater in meadows compared to mixed conifer, plant species composition varied more among meadows and lodgepole pine forests than among mixed conifer forests, resulting in meadows contributing more to the diversity of plant species than mixed conifer forests. The frequent co-occurrence of meadow with lodgepole pine (meadow was present on 76% of all reaches

with lodgepole) makes the combination of these two vegetation types a strong contributor to plant species diversity in the basin.

16. Channel flow had the second highest contribution to overall diversity, showing a shift of over 50% of the plant flora. Channel flow had a similar level of turnover as the forest to meadow gradient, but a slightly lower alpha diversity. Like the forest to meadow gradient, frequency of occurrence declined while species richness increased from segments 1 to 4, thus masking increases in species richness along the gradient.

Management Recommendations

1. The overall richness of plant and the number of plant species per sample reach were comparable to, or greater than, many similar studies of richness and biological diversity in riparian ecosystems at lower elevations. Plants comprise an important food and substrate base for higher trophic levels and managing to conserve their diversity may also serve to maintain their functional role in riparian environments.

2. Based on the curvilinear relationship observed between plant species richness and precipitation, moisture may be the most limiting factor at lower elevations; however, at the highest elevations, temperature or nutrients may become more limiting. Conditions meeting the needs of the greatest number of species occurred at intermediate levels of precipitation, where presumably temperature and soil conditions were also intermediate, and no one of these essential factors was substantially more limiting than another. Areas with average annual precipitation between 110 and 130 cm/yr represent optimum values for plant species richness in the Lake Tahoe basin, and could be used as a trigger for increased consideration of plant species diversity in management activities.

3. Given that plants were more speciose, and a greater proportion of plants were rare on the mesic, west side of the basin, management activities on the west side of basin should apply greater concern and consideration to plant species diversity, particularly in regard to fire management, which can dramatically change soil moisture characteristics.

4. Vegetation characteristics had a substantial relationship with plant species diversity and appeared to be as strongly related as the physical environment. Given that richness and turnover both contributed greatly to the diversity of plant species in the Lake Tahoe basin, conservation of plant diversity would require areas large enough to support the richness of a site, and the establishment of many areas such that the full diversity of vegetation types was represented. A greater number of areas at lower elevations, focusing on meadow, lodgepole pine, and aspen–cottonwood in particular, is called for based on the greater among-reach diversity exhibited by these vegetation types and lower elevation reaches in general.

5. Any effort to conserve the richness and diversity of plant species in the Lake Tahoe basin would benefit from special management considerations for lodgepole pine, particularly in proximity to streams and meadows. The higher richness of aquatic-, riparian-, and meadow-associated plant species in association with lodgepole pine indicates that the occurrence of riparian woodland vegetation may not be a good indicator of environments important in the support of aquatic, riparian, or meadow plant species. In the Lake Tahoe basin, it may be prudent to consider the potential impacts of management on riparian species based not on "indicator" vegetation types, but rather based on a given distance from the stream, potentially modified by slope and aspect. In terms of lodgepole pine management, potential impacts include cattle grazing and fire management. Lodgepole pine is the most common invader in

montane meadows and the lack of fire in the basin may be resulting in a greater prevalence of lodgepole pine forests. Fire is likely to play an important role in maintaining the vigor and diversity of lodgepole pine and meadows, as well as a mutual balance in their extents.

6. Meadows are typically considered highly productive environments, particularly at lower elevations, but in this study they did not individually support a high diversity of plant species. It is probable that historically heavy grazing by sheep and cattle throughout the Sierra Nevada, including the Lake Tahoe basin, combined with continued lower levels of grazing in most wet meadows throughout the basin, impacted the diversity of plant species currently occurring in wet meadow habitats. The greatest threats to meadow condition and extent are lack of fire, which can affect succession, and water diversions and grazing, which can affect the hydrodynamics of meadows. Prescribed fires and wildfires that are allowed to burn should generally improve the quality and quantity of meadows in the basin. Channel restoration efforts should consider potential impacts on meadow systems. Grazing should be carefully managed to avoid negative effects on plant species diversity.

7. Aspen–cottonwood was associated with high plant species richness. Given the high diversity of plant species and relative rarity of aspen–cottonwood in the Lake Tahoe basin, management of these stands could substantially affect plant species diversity. Reaches with greater than 10% of the area occupied by aspen–cottonwood should be managed with consideration for plant species diversity. Maintaining natural processes, such as nutrient cycling, succession, and fire, and minimizing human-related disturbances, such as grazing and mountain biking, are the most likely means by which plant species richness might be conserved in aspen–cottonwood stands. The increased use of prescribed fire and proportion of wildfires that are allowed to burn, and limited or no grazing are measures that are likely to improve the biological integrity and perhaps the extent of aspen stands in the basin.

8. Alder–willow contributed to the richness of aquatic–riparian–meadow plant species. Alder and willow occurred frequently along stream reaches, and were generally well distributed throughout the Lake Tahoe basin. Management activities are unlikely to change the distribution of alder and willow, but grazing and channel restoration could alter associated hydrologic regimes. Key meadow and riparian complexes should be identified throughout the basin, and then restoration efforts that involve key meadow complexes, particularly those with well developed alder and willow vegetation, should be carefully managed so as to avoid detrimental effects.

9. Existing stands of dense, small-diameter snags and logs appeared to have low suitability for some plant species. High turnover along the snag and log gradient suggests that species are variously adapted to woody debris and the occlusion of bare mineral soil, as well as the types of environments with greater or lesser amounts of woody debris. High densities of woody debris, particularly logs, are likely to occlude ambient light from reaching mineral soil, reducing the ability for plants to become established or to maintain themselves. Management of woody debris to benefit plant diversity should focus on reducing uncharacteristically high densities resulting from lack of fire, but otherwise maintaining a range of densities. Fire management to reduce the risk of fire in the Lake Tahoe basin is likely to create more favorable conditions for plant species diversity.

10. Aquatic, riparian, and meadow associates and rare species were more speciose in association with greater channel flow. Because of the sensitivity of plant species to soil moisture and inundation, the typically high variety of microhabitats within a single floodplain can support a

broad array of plant species and assemblages. Competition for the use of floodplains, particularly at the mouths of streams near Lake Tahoe, is high because they are flat and have rich soils. Losses from development are compounded by uses such as grazing and recreation, which can readily impact plant species diversity. Floodplain management should be a key focal point in the conservation of plant species diversity in the Lake Tahoe basin.

MACROFUNGI DIVERSITY IN LOTIC RIPARIAN ECOSYSTEMS

Key Findings

1. I encountered a relatively low number (*n* = 55) of fungi genera, compared to the number of genera identified as potentially occurring in the Lake Tahoe basin (*n* = 339). However, the number of documented fungi genera total only 60 genera, and thus my study encountered over 90% of all fungi genera known to occur in the basin.

2. Richness and turnover had similar magnitude contributions to the diversity of fungi basin-wide. Each reach contained an average of 13% and as high as 29% of the total number of fungi genera observed throughout the Lake Tahoe basin. Similarly, turnover was moderate, averaging 13% and ranging from 9% to 16% of all genera between the lower to upper halves of the 8 environmental gradients examined. Therefore, environmental features that influenced either richness or turnover were important in determining fungi diversity in the Lake Tahoe basin.

3. Lichen genera were the most prevalent fungi life form encountered in my study. The seasonal nature of fruiting-bodies of fleshy fungi made them less detectable than lichen genera, which are physically present all year long. The result was that even though I encountered more fleshy fungi genera than lichen genera, lichen genera were detected on twice as many reaches and the average frequency of occurrence was over 3 times higher compared to fleshy fungi. The 10 most frequently occurring macrofungi consisted of 7 lichen and 3 fleshy fungi, and comprised over 60% of the macrofungi observations.

4. Fungi genera richness was positively associated with channel gradient, subalpine conifer, shrubs, canopy cover index, and large snags. The composite of these variables represent higher elevation areas with more densely forested areas with large woody debris and some shrubs. Similarly, fungi genera richness was positively correlated with the elevation–precipitation and snag and log gradients, and negatively correlated with forest to meadow and channel flow gradients. The snag and log gradient was unique among all gradients in that it was strongly positively associated with the richness of both rare and common fungi, indicating that snags and logs serve as an important substrate for both lichen and fleshy fungi. The richness of the lichen and common fungi groups were significantly positively correlated with subalpine vegetation and canopy cover index.

5. Potential thresholds were observed for lichen richness in association with subalpine conifer vegetation, where at least 2 genera of lichen were consistently present on reaches where subalpine conifer was present.

6. Fungi genera richness was positively correlated with common genera richness and lichen genera richness, indicating that patterns of total richness were driven primarily by common genera.

7. Rare genera richness was positively correlated with fleshy fungi richness, indicating that more fleshy fungi were rare. Rare and common genera richness were not correlated.

8. The richness of fleshy fungi was not strongly related to the environmental conditions described in this study (< 10% of the variation in richness explained). The lack of a relationship between environmental variables and fleshy fungi is most likely a reflection of the relatively high number of fleshy fungi genera combined with their relatively low frequency of occurrence, resulting in a constantly shifting assemblage of fleshy fungi among reaches.

9. No relationships were observed between richness and orientation within the Lake Tahoe basin. This is consistent with the interpretation that fungi richness is responding to finer scale features in the environment, such as snags and logs, which do not vary substantially by basin orientation.

10. Richness and turnover were driven by different environmental features and generally varied in opposition to one another. Richness was primarily associated with channel flow characteristics and coniferous vegetation, whereas turnover was primarily associated with precipitation and riparian woodland vegetation. The opposing relationships of richness and turnover are most likely a reflection of the different environmental relationships of lichen and fleshy fungi, where lichen dominated patterns of richness, and fleshy fungi was primarily responsible for turnover between reaches and gradient segments. Thus, the strong upland vegetation associations of lichen and the most common fleshy fungi (i.e., *Polypore*, *Cryptoporus*, *and Hemitricia*) were expressed in the environmental relationships of most measures of richness (specifically, lichen, common fungi, total fungi richness), and the moisture-related environmental sensitivities and relationships of fleshy fungi were reflected in the gradients associated with turnover.

11. Precipitation, aspen–cottonwood and alder–willow gradients had the greatest influence on fungi genera turnover. Precipitation had the greatest influence on turnover, as well as overall diversity of fungi genera in the basin. The high turnover along the precipitation gradient suggests that genera were somewhat specialized along the precipitation gradient and that turnover was driven by rare genera. No genera with frequencies $\geq$ 10% and no unique genera were absent along the precipitation gradient. Richness and turnover were low in association with elevation; however, when combined with precipitation in the elevation–precipitation gradient, a positive association with richness (total and common genera) was observed.

12. Abiotic environmental features had the greatest overall influence on the diversity of fungi genera, with vegetation types having a strong secondary effect. Precipitation had the greatest influence, followed by channel flow gradient. The channel flow gradient was the only gradient associated with both richness and turnover. Turnover was consistent along the channel flow gradient, and it appeared that more frequent genera (present on 2 or more reaches) were absent from the more extreme channel flow conditions. The pervasive positive influence of channel gradient on richness indicates that fungi genera are more diverse in upland environments than riparian environments, particularly common genera.

13. The aspen–cottonwood gradient was the third greatest contributor to the diversity of fungi genera in the Lake Tahoe basin. Most of the diversity associated with the aspen–cottonwood gradient was contributed by turnover. Thus, aspen–cottonwood provides a specialized environment for fungi, specifically fleshy fungi *Scutellinia* and *Bisporella*.

14. Although the forest to meadow gradient ranked low in turnover, it had the highest number of core turnovers (genera present on more than 1 reach) among segments, and over 7% were associated with genera not occurring in the meadow–lodgepole pine portion of the forest to meadow gradient. One genus, *Coprinus*, only occurred in the meadow–lodgepole pine portion of the gradient.

15. Three genera occurring on $\geq$ 10% of the reaches were restricted to a portion of one or more environmental gradients, and may be reaching environmental limits along the associated gradients. *Tyromyces* was absent from the highest channel flow segment and the lower most segment of the forest to meadow gradient. *Tyromyces* is a fleshy fungi that attacks dead or dying conifer trees. *Noleana* was absent from the highest channel flow segment and from the lowest segment of the elevation–precipitation gradient. *Noleana* is saprophytic, growing on the ground or woody debris, and it is most likely limited by the availability of woody material. *Acarospora*, like *Tyromyces*, was absent from the lower-most segment of the forest to meadow gradient. *Acaraspora* is a wide-spread crustose lichen genus occurring primarily on exposed acidic rocks in sunny locations at high elevations. Rocks are far less common in meadows compared to forested environments in the Lake Tahoe basin, and so the lack of available of rocky substrates is most likely to be the reason for its absence from meadows.

16. The alder–willow gradient was associated with relatively high turnover (3rd highest gradient), but was not associated with richness and thus overall had a relatively limited influence on diversity. As observed along the aspen–cottonwood gradient, alder–willow appears to provide a specialized environment for some fungi genera, specifically fleshy fungi *Bisporella* and *Guepiniopsis.*

Management Recommendations

1. Conifer forests were the environment where fungi richness and turnover was greatest. The greatest potential management effects on fungi diversity are from timber harvest and fire management. Timber harvest activities could reduce suitable live and dead tree substrates, and invoke frequencies of disturbance that reduce the ability for fruiticose and foliose lichen to persist and grow. Fire could pose threats to lichen diversity if uncharacteristically large and hot fires occurred, as opposed to a more natural fire regime consisting of more frequent, less intensive fires.

2. Subalpine conifer, a high elevation vegetation type, was positively associated with fungi richness. The positive relationship observed between lichen richness and subalpine conifer probably reflects a high prevalence of both conifers and rocky substrates, the primary substrates of lichens encountered in the study area.

3. The close association between the richness of fleshy fungi and both aspen–cottonwood and alder–willow points toward important considerations the management of these vegetation types. Genera restricted to the upper ends of the aspen–cottonwood and alder–willow gradients may be moisture limited, and management that affects the moisture regime in riparian woodlands could negatively affect fungi diversity in the Lake Tahoe basin. Further, it is possible that the lack of fire has reduced the extent of aspen. The increased use of prescribed fire and proportion of wildfires that are allowed to burn are likely to improve the vigor and perhaps the extent of aspen stands in the basin. Alder and willow occurred frequently along stream reaches, and were generally well distributed throughout the Lake Tahoe basin. Management activities are unlikely to change the distribution of alder and

willow, but grazing and channel restoration could alter its abundance. Restoration efforts that involve key meadow complexes with well developed alder and willow vegetation should be carefully considered so as to avoid detrimental effects on riparian and meadow habitat.

4. Most of the lichen and fleshy fungi genera detected in this study are associated with woody materials, living or dead. Large logs were strongly associated with all measures of fungi diversity, with richness being greater at higher densities of large logs. It is apparent that logs play an important role in supporting a diversity of fungi in the Lake Tahoe basin. Management of snags and logs to benefit fungi diversity should focus on the retention and recruitment of large snags and logs. Future attempts to reduce fine fuels in the Lake Tahoe basin may pose a risk to the quality and quantity of large snags and logs as substrates for fungi. Careful fire management to conserve values provided by large snags and logs would contribute to retaining substrates for fungi.

CROSS-TAXONOMIC DIVERSITY IN LOTIC RIPARIAN ECOSYSTEMS

Key Findings

1. Despite major differences in the life histories and habitat associations within and among taxonomic groups, the same set of macro- and meso-scale environmental variables were effective in describing environmental relationships and patterns of diversity across multiple taxonomic groups. Environmental variables explained 22% to 40% of the variation in richness of individual taxonomic groups, and correlations with individual variables ranged as high as 53%.

2. Taxonomic groups often had opposing relationships with environmental features. Opposing relationships with 2 or more taxonomic groups were observed in association with meadows, conifer forests, elevation, and precipitation. For example, bird and invertebrate richness were closely associated with meadow and lodgepole pine forests, whereas fungi richness was associated with mixed conifer and subalpine conifer forests. Birds were richer at lower elevations, whereas mammals were richer at higher elevations. Finally, plants were richer and birds were less rich in association with higher precipitation, and fungi richness did not change in relation to precipitation but turnover was high.

3. No one environmental gradient had a significantly greater influence on gamma diversity across all taxonomic groups than any other; variation in turnover rates among taxa was so high that it masked differences in diversity among gradients. However, a few gradients were consistently associated with higher diversity. Channel flow, forest to meadow, and precipitation gradients had the greatest influence on both richness and turnover for many taxonomic groups, and thus the majority of diversity in lotic riparian biota in the Lake Tahoe basin lies along these 3 environmental axes. Channel flow reflects shifts from upland to aquatic conditions, the forest to meadow gradient reflects the diversity of vegetation types and structures occurring among low to mid elevation reaches, and the precipitation gradient represents a range of moisture availability including the prevalence of aquatic environments.

4. Across all taxonomic groups and environmental gradients, richness and turnover made similar contributions to diversity, with turnover being responsible for an average of 57% and richness responsible for an average of 43% of overall taxonomic diversity. However, this average represents wide variation in the role of richness and turnover in the diversity of each taxonomic group. Taxonomic groups had inherently different between-site variance in species composition. For example, birds and mammals had much higher richness per reach and lower

turnover rates among reaches than the other 3 taxonomic groups, indicating that neither taxonomic group was highly spatially variable.

5. Environmental gradients associated with the highest turnover were different from those associated with the highest richness, across taxonomic groups, as well as within them. Thus, richness and turnover not only described different facets of diversity, but they also reflected different progenitors of diversity. These results highlight that management based on richness or turnover alone may not be satisfactory in supporting the native diversity of an area.

6. Although most environmental characteristics we analyzed reflected local environmental conditions, it appeared that larger temporal and spatial scale processes, such as emigration, also influenced the composition of taxonomic groups studied. Environmental features classically associated with productivity, namely as elevation and precipitation, were strongly associated with the diversity of many taxonomic groups in the basin. However, apparent increases in productivity were not accompanied by gaining additional taxa, but rather were associated with major shifts in species composition, where some species were lost while others were gained.

7. The many relationships observed among taxonomic groups reflected similarity in their environmental associations, as opposed to interrelationships between taxa. For example, mammals, plants, and lichen richness were all generally positively correlated with one another, and they all appeared to be responding to denser forest conditions (i.e., mixed conifer and subalpine conifer forests). Further, bird, invertebrate, and fleshy fungi richness were all generally positively correlated with one another, and they all appeared to be responding to more open environments (i.e. meadows and lodgepole pine forests).

8. A few inter-taxonomic correlations potentially reflected interrelationships. For example, it is plausible that the increase in bird species richness associated with increased invertebrate family richness reflects a response to invertebrate food availability. Most songbirds rely on invertebrates for some portion of their diet, and may be responding to invertebrate biomass. If birds are at least partly responding to richness of invertebrates, then the environmental features associated with invertebrate richness (such as meadow and lodgepole pine) may have the potential to indirectly affect bird species richness.

9. Similarly, higher Lepidoptera genera richness was associated with plant species richness, which could reflect an interrelationship between butterflies and plants. Butterflies and moths are typically stenotypic in their plant species associations, and some are associated with only one plant species, so it is likely that plant species richness would support a greater variety of butterfly and moth species. The fact that Lepidoptera richness showed virtually no relationships with any of the environmental features analyzed lends further credence to the notion that the observed relationship between Lepidoptera and plant richness is not an artifact of related environmental features.

10. Despite moderately strong correlations in the richness of some taxonomic groups, individual taxonomic groups were not good predictors of the diversity of other taxonomic groups. Greater variation in diversity among taxonomic groups versus among gradients, and the large proportion of variation (over 70%) unexplained in correlations between any 2 taxonomic groups provides evidence of the inadequacy of any one taxonomic group’s ability to represent the richness and diversity of other taxonomic groups.

Management Recommendations

1. The Lake Tahoe basin is a unique environment within the Sierra Nevada, and it is of high social value because of its beauty and environmental diversity. The first step toward conserving biological diversity in an area such as the Lake Tahoe basin is to understand (to the extent possible) the conditions that support a full suite of native biota. The second step is then to apply this understanding to the design and implementation of a conservation strategy to maintain and restore biological diversity.

2. Results of my study showed that biological diversity in stream-side environments is strongly responding to abiotic, meso-scale environmental features associated with channel characteristics. It is noteworthy that between the effects of channel gradient, width, and sinuosity, the richness of every taxonomic group was affected in some manner by channel flow characteristics. Conservation and restoration efforts focused on in-stream conditions and biota should take into consideration the potential impact they may have on riparian-associated biota.

3. I found that precipitation and elevation (to a lesser degree) were associated with high levels of turnover, and had opposing relationships with richness of birds, mammals, and plants. Although management does not typically affect precipitation over short time periods, the relationship between diversity, precipitation, and elevation has management implications in terms of being important gradients to be represented in areas identified for the conservation of biological diversity in the Lake Tahoe basin.

4. Meadows supported a rich and diverse array of taxa. Given that meadow occurred on less than half of the sample reaches, it is clear that meadows play an important role in supporting biological diversity in the Lake Tahoe basin, and that meadow management alone could substantially affect biological diversity. Wet meadows in an upper montane and subalpine environment provide a unique and rich array of resources for all but the most stenotypic forest associates. A greater diversity of plants, in addition to birds and invertebrates, would potentially result from an increase in the quality and quantity of meadows in the basin. Most lichen genera and certain mammal species (e.g., Douglas squirrel, golden-mantled ground squirrel) were some of the few taxa that would not benefit directly from managing meadows for biological diversity.

5. Potential threats to the quality and quantity of meadows include grazing, lack of fire, and channel restorations. Deleterious effects from grazing may be reduced by invoking seasonal restrictions on grazing in meadows with the highest potential for supporting high biological diversity; however, some studies suggest that grazing must be eliminated for some period of time to effectively restore meadow function. Fire strongly influences the function and maintenance of meadows in the Sierra Nevada. Increased use of prescribed fire in the basin should improve the quality and quantity of meadows if burns are light such that soil moisture conditions are not altered. Channel restoration could affect meadow conditions, as well as alder and willow abundance. Restoration efforts that involve key meadow complexes with well-developed alder and willow vegetation should be carefully considered so as to avoid detrimental effects on riparian and meadow environments.

6. The high value of lodgepole pine to taxonomic richness is in contrast to generally held perceptions that lodgepole pine stands provide habitat for relatively few species because of their structural simplicity. Duality of this species' life history, growing both in mesic environments and xeric, high elevation sites may be responsible for this apparent contrast. In

this study, all lodgepole pine stands sampled were in mesic environments in association with streams. Potential management impacts include cattle grazing and fire management, and an assessment of the interaction of grazing and fire with key features of lodgepole pine stands would provide valuable insights into how best to manage lodgepole pine stands to conserve biological diversity.

7. Riparian woodland vegetation, namely alder–willow and aspen–cottonwood, contributed to the support of a diversity of biota. The management of these vegetation types will substantially affect the diversity of most macrobiota using stream-side riparian areas in the basin. Conservation efforts should not assume that more alder–willow and aspen–cottonwood will necessarily enhance biological diversity, but rather they are important gradients to be represented in areas identified for the conservation of biological diversity in the Lake Tahoe basin. Further, the quality of alder–willow and aspen–cottonwood could be affected by management activities such as grazing, fire management, and channel restoration.

8. The varied interrelationships of richness among taxonomic groups provide insights into how best to design conservation approaches. The richness of birds, invertebrates, and fleshy fungi all followed similar patterns in association with environmental features, and were closely associated with more open-canopied environments, particularly meadows. Conversely, the richness of mammals, plants, and lichen were all similarly associated with more upland, forested environments. Conservation of meadow environments, for example, should take into consideration the array of closely associated biota and general considerations in support of their diversity.

9. Although correlations in diversity do exist between some species groups, the relationships rarely correspond closely enough to serve as useful indicators for one another. Thus, the potential of greatly simplified environmental inventory or monitoring efforts through the employ of indicator species groups does not appear to be a viable option in the Lake Tahoe basin. To the contrary, changes in patterns of richness among taxonomic groups provide valuable insights into the biotic and abiotic processes driving changes (or lack thereof) in biological diversity within and among taxonomic groups. They also represent a greater array of ecological diversity (the variety of ecological roles, diet components, and microhabitat uses exhibited by an assemblage of species) and morphological diversity (the variety of physical characteristics of species), which can be mined through analysis to gain additional information on trends in diversity and insights into the environmental factors driving observed trends.

10. Differences among taxonomic groups in their associated environmental features indicate that one or even a few environmental features would not be sufficient indicators of biological diversity across taxonomic groups. In riparian environments in the Lake Tahoe basin, it was clear that taxonomic groups were responding to a variety of environmental features, both biotic and abiotic. The distribution and abundance of vegetation types did not track patterns of variation for other biotic and abiotic environmental features that surfaced as major influences on biological diversity. It is still possible that indicators of richness and diversity could be found or developed, but data collection and analysis would have to structured to query specifically for sufficiently robust relationships.

ENVIRONMENTAL CHARACTERISTICS OF LENTIC RIPARIAN ECOSYSTEMS

Key Findings

1. Lentic units at a wide range of elevations and precipitation levels and in a wide range of sizes were sampled. Lentic units sampled ranged from < 0.1 ha to 570 ha, and from 0.1 m to > 100 m deep. The 88 sample units varied widely in the amount of disturbance within 200 m, as measured by an index of road density, although most sample units had low disturbance. Disturbance was higher at low elevations and near meadows.

2. The primary vegetation gradient associated with lentic sample units reflected the influence of elevation, from mixed conifer at lower elevations to subalpine conifer forest and shrubs at higher elevations.

3. The gradient of aspen to meadow represented the second vegetation gradient surrounding lentic ecosystems even though aspen was the least common vegetation type. Aspen and meadow are unique and uncommon ecosystems that require slightly different soil moisture regimes.

4. A wide variety of substrate types was observed, indicating the potential for a range of productivity of lentic units and available habitat elements. Substrate may influence the occurrence and abundance of a variety of taxa.

5. Overhanging vegetation and floating and submerged logs provide cover for amphibians, invertebrates, and potentially many other aquatic organisms. Both were highly variable among lentic units, indicating a range of available cover for aquatic biota.

6. Several environmental characteristics varied among the 4 basin orientations. The west side of the basin was characterized by steeper, rockier terrain with a greater range of elevations and precipitation than the other sides of the basin. The east side was generally more disturbed than other sides of the basin, suggesting that effects of disturbance on biological diversity will be displayed the most profoundly on the east side. The north and south sides of the basin were usually intermediate in environmental characteristics.

BIOLOGICAL DIVERSITY IN LENTIC RIPARIAN ECOSYSTEMS

Key Findings

Bird Diversity

1. Lentic ecosystems in the Lake Tahoe basin provide habitat for a variety of bird species—a total of 93 native species were detected, with nearly 45% of these primarily associated with aquatic, riparian, and meadow ecosystems.

2. Aquatic bird diversity increased near meadow vegetation. Riparian–meadow birds were more diverse near meadows, riparian vegetation, and aspen, ecosystems that are known to support a wide variety of bird species. Though upland birds were also associated with riparian vegetation, their associations were stronger with shrubs and canopy cover.

3. The negative relationship observed between elevation and the alpha diversity of all birds suggests that diversity was lower in the harsh conditions (e.g., high winds, low temperatures) at high elevations. When birds were examined by habitat group, aquatic and riparian–meadow

birds showed a decrease in diversity at higher elevations, but upland birds did not, as was the case for birds in lotic ecosystems. Fewer than 1 aquatic bird species per point count were detected above 2600 m in elevation and aquatic birds were absent above 2800 m. Sample units > 2600 m in elevation had an average of ≤ 1 riparian–meadow bird species per point count.

4. In general, bird diversity was greatest at sample units on the east side and lowest at sample units on the west side of the basin.

5. Aquatic birds were absent at sample units with high log densities (> 46.5% frequency).

6. Aquatic birds were generally absent at sample units smaller than 0.1 ha and ≤ 2 aquatic birds occurred at sample units smaller than 0.5 ha.

7. More species were present at large sample units. Part of this relationship may be attributable to a bias of increased sampling, but in addition, larger sample units are likely to encompass a wider range of habitats and therefore a larger array of species.

Amphibian Diversity

8. No strong predictors of amphibian species richness were evident in this study. However, richness was generally lower in deep sample units with rocky substrates and higher in sample units with silt substrates. No amphibians occurred at sample units where the substrate was ≥ 20% cobbles.

Littoral Zone Plant Diversity

9. By far, the factor most closely associated with littoral zone plants in this study was the relative abundance of silt substrates. Plants were more common and more diverse in silt substrates than in any other substrate type, and were negatively related to all other substrate types.

10. Sample units surrounded by riparian and meadow vegetation supported a diversity of littoral zone plants.

Management Recommendations

1. Focusing conservation efforts on larger lentic sample units, especially ones on the east side and at lower elevations, will provide the greatest benefit to supporting the biodiversity of aquatic and riparian–meadow birds. Rare species may not be entirely accommodated by this conservation approach; additional conservation efforts may be needed.

2. The species richness of amphibians in species-poor environments may not be very sensitive measures of a site's productivity or ability to support biological diversity.

3. Future efforts to determine environmental relationships of littoral zone plants in the basin could benefit from additional field measurements that were beyond the scope of this study. For example, various measurements of water chemistry, such as dissolved oxygen, pH, and the presence of certain ions, have been shown to affect aquatic plant species composition.

4. The varying patterns of diversity observed for the different taxonomic groups suggest that taxon-specific management strategies will likely be necessary.

Single-species Relationships in Lotic and Lentic Riparian Ecosystems

Key Findings

1. Brown-headed Cowbirds were among the most common birds detected, occurring at 78% of sample reaches and 28% of lentic sample units. In both lotic and lentic riparian ecosystems, cowbirds were more common at low elevations, near meadows, and on the east side of the basin. Cowbirds in lentic ecosystems were in low abundance at elevations > 2000 m and absent above 2600 m. Cowbirds were also associated with high human disturbance in the vicinity of lentic ecosystems.

2. Beaver activity was observed in 11 of 20 watersheds. Beavers were present more frequently in low elevation, low gradient, wide reaches close to the mouth of streams. Beavers were not detected in streams < 5 m wide. Vegetation associations indicated that beaver presence was associated with more open valley forms, as indicated by the association with meadow and lodgepole pine vegetation.

3. Pacific treefrogs were detected at nearly one-half of all sample units and were by far the most frequent and abundant amphibian in our surveys. Treefrogs were more abundant at small, shallow sample units with silt substrates and plenty of littoral zone vegetation. Treefrogs were in low abundance at sample units > 4 m deep and absent from sample units > 13 m deep. In addition, treefrogs tended not to occupy lentic units with trout.

4. Western toads were relatively uncommon across sample units, and thus few environmental relationships of western toads were revealed. Toads were associated with a range of elevations and substrate characteristics, consistent with their characterization as habitat generalists.

5. Long-toed salamanders were detected infrequently, and no environmental relationships could be determined. However, it appeared that salamanders did not occupy lentic units with trout. The detection of long-toed salamanders at Edgewood Lake was a significant finding—the first record of native salamander in Nevada.

6. Bullfrogs were also detected infrequently, but quite clearly at low elevation lentic units with high human disturbance on the south side of the basin. Bullfrogs occur in some areas in the basin that may allow them to expand to higher elevations.

7. We detected mountain yellow-legged frogs at 2 lentic units in the basin; to our knowledge, our observations of larvae at both lentic units constitute the only records of yellow-legged frog breeding in the basin in several decades. Both sites appear to be suitable mountain yellow-legged frog habitat because they are permanent water bodies with a depth of at least 2 m in some places and have no trout, critical habitat features for mountain yellow-legged frog breeding populations.

8. In lentic ecosystems, garter snakes were most frequently associated with larger, deeper lakes with rocky substrates, abundant logs, fish, and sparse littoral zone vegetation. Garter snakes occurred more frequently in association with fish, suggesting that fish are a primary prey item. In lotic ecosystems, garter snakes were most frequently associated with low elevations, low canopy cover, and wider channels. Garter snakes were not detected at sample reaches > 2100 m in elevation or with canopy cover > 60%.

Management Recommendations

1. Cowbird management may be warranted in the basin, but additional work needs to be done to better define the scope of the problem. Recommended steps include assessment of cowbird presence, density, and of patterns of occurrence, and determination of the degree to which parasitism affects species of concern, including effects on the reproductive success of hosts.

2. Efforts to reduce and remove beaver from some watersheds should probably concentrate on watersheds that are relatively ecologically intact (e.g., not dammed, no artificial channel alterations, relatively undeveloped) and that have suitable habitat for beaver. In the remaining watersheds, watershed conservation measures might include determining where beaver are doing the most damage to channel conditions and biota, and keeping populations in these watersheds at minimum levels. Beavers could be relocated to watersheds where their populations will be more resource limited, such as small sized watersheds with more narrow channel widths and higher gradient channels. Other management techniques, such as dam removal, may be effective in reducing the potential for ecological damage without moving or threatening the viability of individual or populations of beaver.

3. The differing patterns of association for the basin's native amphibians suggest that, generally speaking, habitat restoration targeted at a single amphibian species is unlikely to improve conditions for other amphibian species. However, most of the native amphibian species appeared to be limited by the presence of trout, based on evidence presented here and in other studies. Eradication of nonnative trout from a subset of the basin's lentic ecosystems, perhaps at the scale of watersheds, is likely to be the single most effective management tool for conserving and restoring the basin's amphibian populations.

4. Further research is needed on amphibians in the basin. Studies that examine the relationship of pond permanence, trout presence, and long-toed salamander occurrence are needed, as are surveys to better document the extent of salamanders in Nevada. Studies determining the extent of bullfrog distribution in the basin and identifying areas at greatest risk of invasion need to be conducted.

5. The persistence of mountain yellow-legged frog populations in the basin appears to be at risk, with only a single known population. Additional sites may need to be colonized, possibly by reintroduction, coupled with eradication of exotic trout from some sites. An analysis of suitable habitat within the basin would be an appropriate first step. Then, the benefits of trout eradication to multiple amphibian species could be examined.

6. Because garter snakes are suspected to be in decline, further research would be useful to elucidate patterns of occurrence and differences in habitat associations among the basin's 3 species. Small sample sizes precluded more definitive information on garter snake species.

SUMMARY RECOMMENDATIONS

1. A landscape-scale conservation approach is necessary to address the conservation of multiple taxonomic groups associated with lotic and lentic riparian ecosystems in an area the size of the Lake Tahoe basin. Basic considerations in the design of conservation reserves include the following 6 issues: (1) how large should they be (single large or several small)?; (2) do they encompass the spatial and temporal heterogeneity and dynamics of the landscape (minimum dynamic area)?; (3) how does the surrounding "matrix" affect the quality of the reserve?; (4) are major landscape features connected in a manner that facilitates movement of biota?; (5)

should landscape features that have been modified be included in the reserve design?; and (6) are buffer zones needed or desired around reserves (multiple-use modules)?.

2. The relatively equivalent contributions of richness and turnover to biological diversity observed in lotic ecosystems indicate the need for a broad, landscape approach to conserving biological diversity in which the majority of the basin is managed with an eye toward the conservation of biological diversity. However, it is not socially desirable nor economically feasible to devote the entire landscape to the primary purpose of conserving biological diversity. Rather, special consideration of the 6 reserve design issues, combined with current human uses and needs, will be required in the design of a strategy to conserve biological diversity in the basin. Bioreserves are a regionalized network of individual preserves as core sites integrated within a series of concentric zones acting as successive buffers or corridors to the core sites. Bioreserves, analogous to biosphere reserves and reserve networks, could be established based on the environmental features identified as associated with high diversity for one or more taxonomic groups. Buffer areas could be designed based on a balance of societal demands and the vulnerabilities of focal taxa.

3. The fact that many macro- and meso-scale environmental variables were moderate to strongly associated with the diversity of taxonomic groups suggests that such environmental variables could be used as the basis for the establishment and management of reserves and buffers throughout the Lake Tahoe basin. For taxonomic groups with lower turnover among sites, such as birds and mammals, identifying areas with environmental conditions associated with high richness is likely to provide for the majority of species. For lotic ecosystems, stream lengths with low gradients and wider channel, meadows, and aspen–cottonwood stands would be the targets for bioreserves for the purposes of conserving bird and mammal diversity, with buffers being focused on protecting habitat quality, such as minimizing disturbance to ground-nesting birds. For lentic ecosystems, large units with surrounding meadows, riparian vegetation, and aspen stands would be the targets of bioreserves for conserving bird diversity, while the varying associations of amphibian taxa suggest that samples of all types of lentic ecosystems (large, fishless lakes; small ponds; bogs; wet meadows) would need to be represented as core sites.

4. Predictive models could potentially be developed to specifically identify areas of high bird or mammal richness, which could then serve as core areas for bioreserves (see Manley et al. 2000). Given the large amount of unexplained variation in the diversity of most taxonomic groups, it is advised that conservation strategies be designed to validate and improve upon the current understanding of environmental conditions that support biological diversity in the Lake Tahoe basin.

5. Taxonomic groups with the highest turnover among sites, such as invertebrates, plants and fungi, are the most challenging to conserve because essentially every site may be important for supporting one or more rarely occurring taxa. Issues of heterogeneity and connectivity become highly relevant. The establishment of a set of bioreserves that encompassed the range of biotopes in the basin would go a long way toward conserving heterogeneity as represented by a breadth of vegetation and aquatic community types. Buffer size and management might be based primarily on the vulnerabilities and natural disturbance regimes of the biotopes because of the broad array of taxa they were established to support.

6. The investigation of both alpha and beta diversity provided valuable insights into how various environmental features affected biological diversity. Assessing both alpha and beta diversity appears to provide a sound foundation for designing strategies to conserve biological diversity,

particularly where the conservation of many taxonomic groups in a heterogeneous environment is of interest.

7. This study showed that richness measures can mask trends in richness depending on how they are analyzed. The interface of alpha and beta diversity lies at the scale at which spatial variation is described. In the study of lotic ecosystems, spatial variation was described at one primary scale, that is between segments along the length of each environmental gradient. Spatial variation within each segment was not a focus of this study, but for the most speciose taxonomic group (plants), within-segment variation revealed differences in richness along the gradient that were not revealed at the reach scale. Analyses addressing both alpha and beta diversity rarely employ more than one scale of analysis for beta diversity; however, valuable information on the patterns of diversity could be lost or misinterpreted by a single scale of analysis for beta diversity.

8. Differences in detectability among taxonomic groups will affect the resources required to monitor various groups, but a breadth of species groups is essential for a robust monitoring program. Some taxonomic groups are more difficult to detect than others, and some members of every taxonomic group will be difficult to detect for one or more reasons. Such species or species groups may require a disproportionate share of resources for monitoring efforts if the desire is to equally represent all species in a taxonomic groups. Monitoring efforts attempting to address patterns of diversity across taxonomic groups may be able to develop correction factors for detectability which adjust observed values based on expected values. Expected values could be derived through a variety of field and analysis techniques.

9. The conservation of biological diversity is a complex undertaking, and the consideration of many taxonomic groups and sources of diversity exacerbates the difficulty of the task. However, it is maintaining and restoring this same complexity that is the ultimate goal of conservation, and grappling with this complexity may be the only means by which conservation efforts have a chance of retaining the function, as well as the presence, of biota in ecological systems. The fate of biological diversity in riparian ecosystems of the Lake Tahoe basin will depend on the ability of agencies and the public to move forward with conservation efforts in the face of imperfect knowledge, and to continue support for efforts to gain better information over time.